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FOSSIL HELODERMA (REPTILIA, HELODERMATIDAE)

By

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Fossil helodermatid lizards are rare. Gilmore (1928:89) described *Heloderma matthewi*, based on a maxillary fragment from the Middle Oligocene of northeastern Colorado. Hoffstetter (1957) described a new helodermatid genus *Eurheloderma* from the Late Eocene and Early Oligocene "Phosphorites du Quercy" of France and De Bonis et al. (1973) reported an unidentified helodermatid from the Phosphorites du Quercy locality at Escamps.

While curating the University of Nebraska State Museum fossil lizard collection I discovered a partial Oligocene *Heloderma* skull, and Larry D. Martin, Museum of Natural History, The University of Kansas, has provided a complete *Heloderma* maxilla from the Oligocene of northeastern Colorado. These new specimens clearly demonstrate that *H. matthewi* is specifically distinct from the living species, and suggest that *Eurheloderma* is not generically distinct from *Heloderma*.

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tions during the research and critically read the manuscript. Mylan Stout kindly helped me in preparation of Figures 1-3, and Martha Haack prepared Figure 4.

Methods

The following recent skeletons were examined: KU 1129, 23008, 23009, AMNH 56432, 72748, 109521, 73835, 71082, 72999, 74778, 72908, 74777, 73771, 72646, 71864, *Heloderma suspectum;* AMNH 57768, 57863, 64128, 56439, *Heloderma horridum.*

Osteological terms are from Oelrich (1956), McDowell and Bogert (1954), and Bogert and Del Campo (1956). All measurements are in millimeters.

Museum abbreviations used with catalogue numbers are as follows:

AMNH	American Museum of Natural History
KU	Museum of Natural History, University of Kansas
UNSM	University of Nebraska State Museum

Systematic Accounts

Class **REPTILIA** Linnaeus, 1758

Order **SQUAMATA** Oppel, 1811

Superfamily **VARANOIDEA** Camp, 1923

Family **HELODERMATIDAE** Gray, 1837

Heloderma Wiegmann, 1829

Trachyderma Wiegmann, 1829
Heloderma Wiegmann, 1829
Eurheloderma Hoffstetter, 1957

Type Species.—*Trachyderma horridum* Wiegmann, 1829

Included Species.—The type species and *H. suspectum* Cope, 1869, *H. matthewi* Gilmore, 1928, and *H. gallicum* (Hoffstetter, 1957).

Discussion.—Hoffstetter (1957) described a new genus and species of the Helodermatidae, *Eurheloderma gallicum,* from the Late Eocene and Early Oligocene "Phosphorites du Quercy" of France. *Eurheloderma* was distinguished from *Heloderma* by an elongate parietal, which is narrow in the middle part, by large, irregular, granular osteoscutes, which are separated by less distinct grooves, and by the poorly developed venom groove (p. 785). Little information was then available on the osteology of the only other known fossil helodermatid, *H. matthewi,* from the Oligocene of North America. New fossil specimens of *H. matthewi,* which are described below, bridge the morphologic and taxonomic gaps between *Eurheloderma* and *Heloderma.* I regard the criteria employed by Hoffstetter in erecting *Eurheloderma* as insufficient to separate that taxon from *Heloderma.* The few differences between

these taxa pertain to the more primitive nature of *E. gallicum.* The overall morphologic similarities between *E. gallicum, H. matthewi, H. suspectum,* and *H. horridum* are more impressive than the differences. Therefore, I have included all four taxa within the genus *Heloderma.* I believe this taxonomic arrangement best depicts the phylogenetic relationships of these helodermatid lizards.

Heloderma matthewi Gilmore, 1928
Figures 1-3

Holotype.—AMNH 990A, posterior part of left maxilla with three teeth.

Type Locality.—Lewis Creek, Logan Co., Colorado.

Stratigraphic Occurrence.—Oreodon beds, White River Formation (=Cedar Creek Member, White River Formation, Galbreath, 1953).

Age.—Middle Oligocene (Orellan), approximately 30-32 million years before present (Berggren, 1972).

Referred Specimens.—KU 7652, complete right maxilla, from Logan Co., Colorado, White River Formation, probably Middle Oligocene (Orellan). UNSM 50011, partial skull represented by right maxilla, frontal, partial parietal, partial right jugal, right postfrontal, partial right pterygoid, partial right prefrontal, partial basisphenoid, supraoccipital, partial quadrate, isolated osteoscutes, and a partial right dentary, from 1½ miles north, ¼ mile west of Redington, Morrill Co., Nebraska, Brule Member, White River Formation, Late Oligocene (Whitneyan).

Revised Diagnosis.—*Heloderma matthewi* differs from *H. suspectum* and *H. horridum* in having 11 maxillary teeth, a venom groove that is indistinct near the base of the teeth, a triangular-outlined frontal, smaller, non-tuberculate osteoscutes and shallow grooves separating adjacent osteoscutes. *H. matthewi* differs from *H. gallicum* in having maxillary osteoscutes separated by shallow grooves, a less constricted parietal at the midpoint, and larger overall size.

Description.—A general description of the maxilla is presented since no significant differences occur between the holotype and referred specimens (Fig. 1). The maxilla ranges in length from 18 (KU 7652) to 22.5 mm (UNSM 50011). The preserved sutural connections of the maxilla are anterolaterally with the premaxilla, and posterolaterally with the jugal. The posterolateral margin of the maxilla does not form part of the orbit, implying that a lacrimal and prefrontal probably lie posterior to the maxilla, as in the living species. The internal articulations are not known. The flattened anterodorsal margin of the maxilla forms the ventral margin of the external naris. The nasal process rises steeply behind the reduced anterior border and curls slightly inward, producing an internal de-

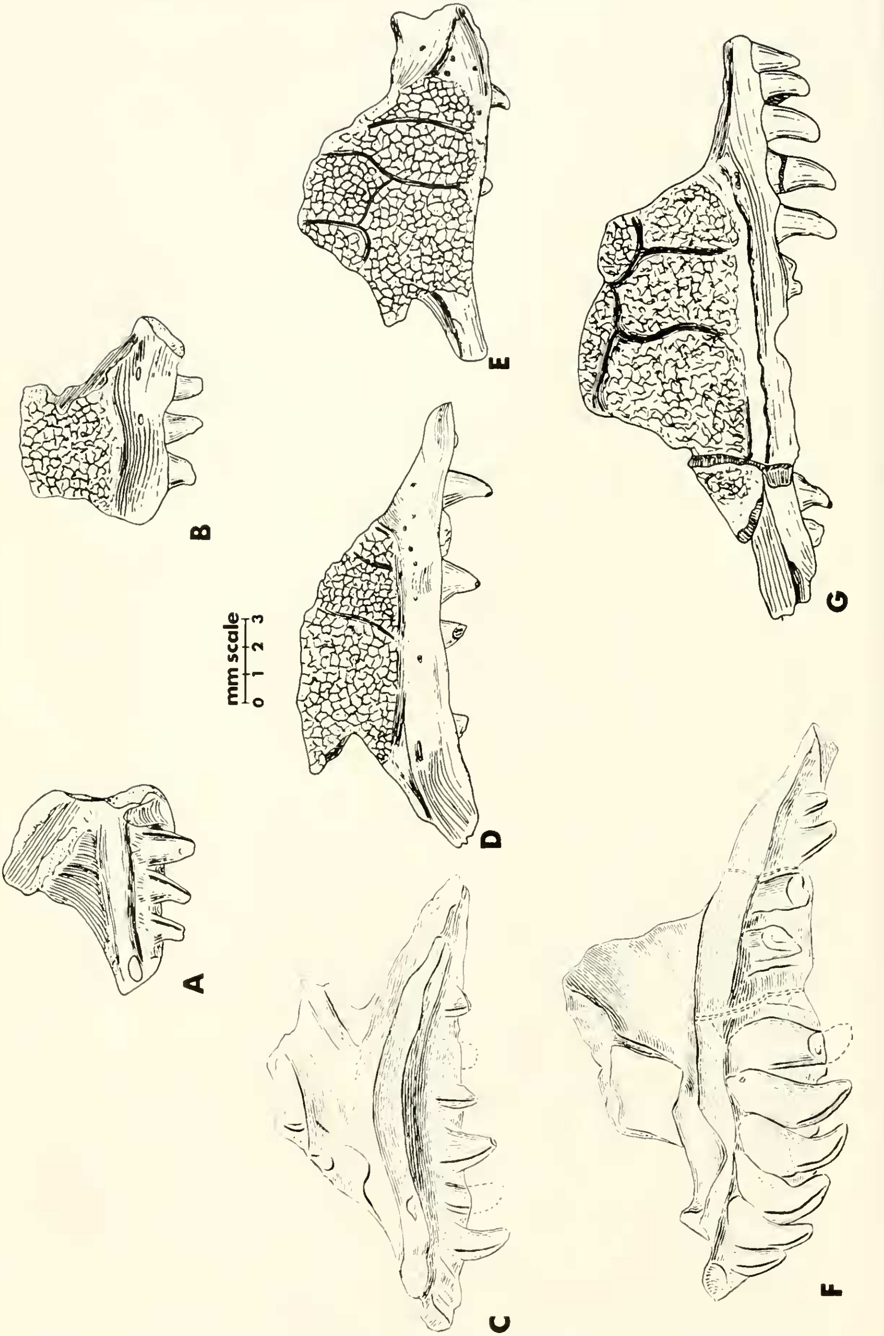

FIG. 1.—*Heloderma matthewi.* A-B. AMNH 990A, Holotype, fragment of left maxilla, internal and external views; C-E, KU 7652, right maxilla, internal, external and dorsal views; F-G, UNSM 50011, right maxilla, internal and external views.

flection of the maxilla. The dorsal margin of the maxilla tapers slightly anteriad. The posterolateral margin of the maxilla is slightly notched and gradually tapers to a posterior point. When viewed dorsally the maxilla is convex externally; the internal margin is more convex than the external margin. There is a distinct open groove developed on the dorsal margin of the palatal shelf for the maxillary artery. The anterolateral suture with the premaxilla is slightly notched. The external surface is slightly convex and is covered by osteoscutes fused to the bone. The osteoscutes end near the ventral margin leaving a small, non-osteoscute area bearing small foramina. The irregularly-shaped granular-textured osteoscutes are relatively large compared to those on the frontal. The grooves between adjacent osteoscutes are shallow.

The maxillary teeth occupy the external edge of the palatal shelf. This shelf narrows near the center of the dental series and has a slight ventral expansion with solid, posterolingually expanded tooth bases, which bear a fluting of fine longitudinal grooves and a basal foramen located on the lingual margin. Tooth replacement is of the anguimorphan type (McDowell and Bogert, 1954:102-103). The tips of the teeth are not sharply pointed. The anterior and posterior teeth are smaller than those at the center of the dental series. Each tooth possesses a venom groove on its anterolingual surface, extending from near the base of the tooth to approximately the tip. The degree of development of the venom groove varies, depending on which tooth is observed, although the groove is more distinct both near the center of the shaft and near the middle of the dental series. It is formed by the slight overlap of the anterolingual surface by the labial surface of the tooth. The tooth crown is approximately circular in cross-section and appears to have no shearing edges.

The frontal is triangular in outline and completely covered with osteoscutes (Fig. 2A). The preserved sutural connections of the frontal are anteriorly with the nasals, posteriorly with the parietal, and laterally with the postfrontal and the prefrontal. The frontal forms the dorsal margin of the orbit. The fronto-nasal suture extends along the anterior margin of the frontal to the point where the prefrontal articulates with the frontal, suggesting that the extreme posterior border of the external naris did not reach the frontal. The anteriorly-directed descending processes of the frontal are well developed and, although broken, probably met at the midline. The arch formed by the juncture of the descending processes is dorsoventrally compressed. The flattened, non-tuberculate, granular-textured osteoscutes on the frontal are smaller than those on the maxilla and the grooves between adjacent osteoscutes are slightly deeper.

Only the anterior half of a left parietal is preserved. The dorsal surface is covered with osteoscutes similar to those on the frontal.

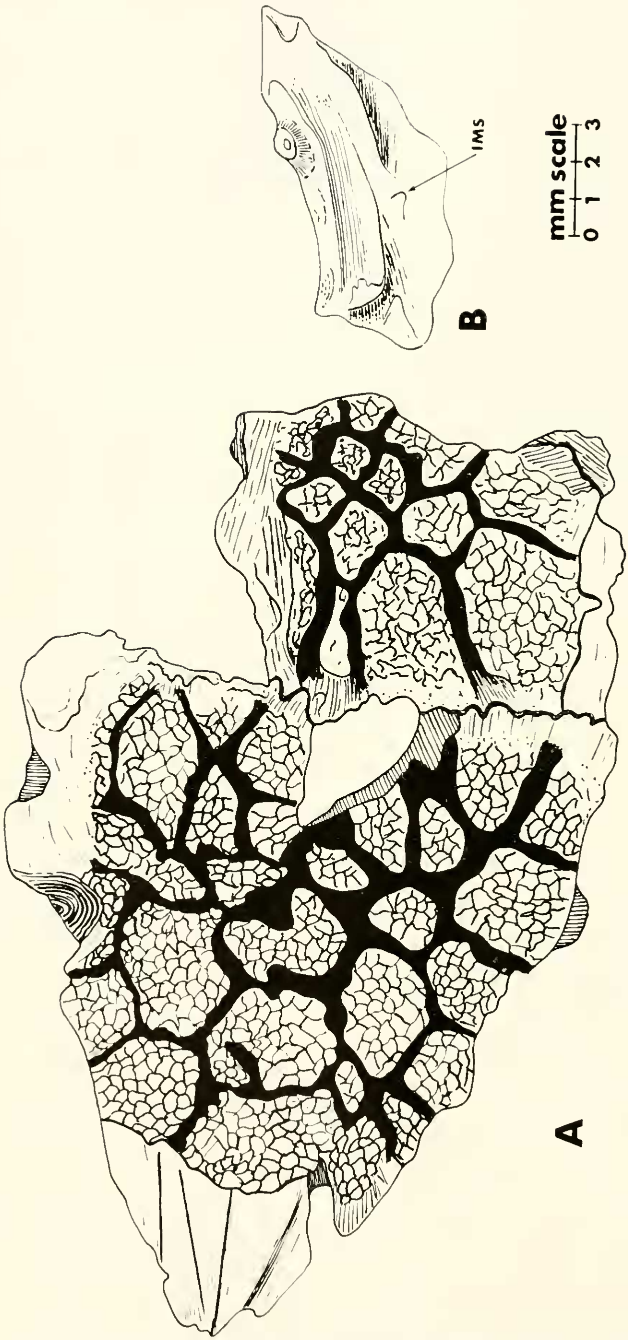

FIG. 2.—*Heloderma matthewi*. A. UNSM 50011, complete frontal and partial parietal, dorsal view; B. UNSM 50011, partial right dentary, lingual view; IMS, intramandibular septum.

There is no indication of a parietal foramen. The central part is almost as wide as the anterior end. There is a weak, obliquely oriented ridge developed on the ventral surface.

A partial rectangular-shaped prefrontal is covered by a large, granular osteoscute. The internal surface is slightly pocketed.

The jugal fragment is rectangular-shaped, owing to the broken posterodorsal extension. The dorsal margin of the jugal forms the ventral margin of the orbit and the lower part of the postorbital bar. There is a groove on the ventral surface, which articulates with a ridge on the posterodorsal surface of the maxilla. There is a distinct angular process where the jugal swings in a dorsal direction. The jugal bears granular, poorly defined osteoscutes.

The postfrontal is a small, square-shaped bone articulating with the frontal, parietal, and jugal. It forms the dorsal part of the postorbital bar and the posterodorsal margin of the orbit. The external surface is irregular, indicating presence of an osteoscute. The relatively large postfrontal and jugal indicate that *H. matthewi* had a complete postorbital bar.

Only the central part of a right pterygoid is preserved. It is angulate, with an externally directed anterior and posterior extension. There is a deep groove on the dorsal surface. The broad, ventrally directed, ovoid-shaped basipterygoid process of the basisphenoid articulates with this groove. The ventral surface of the basisphenoid is flat.

The supraoccipital is a massive bone that bears a slight crest along its dorsal surface. The dorsal surface tapers ventrally and laterally. The posterior margin of the supraoccipital forms the dorsal surface of the foramen magnum.

A partial right dentary has only three tooth bases preserved (Fig. 2B). The tooth bases are round and weakly striated and there is no indication of a venom groove at the base of the teeth. The Meckelian canal is broadly open. In lingual view, the ventral border of the intramandibular septum is partially free. The external surface is smooth and slightly concave. There is a slight posterolateral depression that may indicate an area where the coronoid overlapped the dentary.

Comparisons.—Gilmore (1928:89) separated *H. matthewi* from the living species, *H. suspectum* and *H. horridum*, because of the granular sculpture on the maxilla and the uniformly open anterior groove on the teeth. Bogert and Del Campo (1956:57) considered the granular surface texture as diagnostic of *H. matthewi*. The openness of the anterior groove is subject to considerable individual, age and tooth position variation in the living species. In the living species the venom groove is broadly open near the base of the tooth, uniformly open through most of the shaft length and slightly closed near the crown tip. The specimens newly referred to *H. matthewi* indicate that the venom groove is not broadly open near

the base of the tooth as in the living species. The granular sculpture on the holotypic specimen of *H. matthewi* is actually the remnant of a large, granular osteoscute that was fused to the bone. The specimens referred to *H. matthewi* confirm the presence of a large, shallow, granular-textured osteoscute located in the same area as the sculpture on the holotype. The relatively larger, granular osteoscutes on the maxilla that are separated by shallow grooves in *H. matthewi* are distinct from the smaller, tuberculate, distinctly separated osteoscutes of the living species.

The morphology and the number of maxillary teeth of *H. matthewi* are distinct from the living species. In contrast to *H. suspectum,* which has 8 or 9 maxillary teeth, and *H. horridum,* which has 6 or 7 maxillary teeth, *H. matthewi* has 11 maxillary teeth. The overall shapes of the teeth of *H. matthewi* are much stouter, and they lack distinct cutting edges. The tooth bases are much more bulbous in *H. matthewi* than in the living species (Fig. 3). The venom groove in the living species has a distinct basal expansion, whereas the groove in *H. matthewi* is essentially closed at the base of the tooth.

The maxilla of *H. matthewi* is more similar in shape to that of *H. suspectum* that to *H. horridum.* The nasal process of the maxilla rises at less than 90 degrees in *H. suspectum* and *H. matthewi,* whereas the rise in *H. horridum* is perpendicular or slightly curved in an anterior direction. The internal maxillary fossa is somewhat pocketed and much deeper in *H. horridum* than in *H. suspectum* and *H. matthewi.* The internal posterior margin of the prefrontal is less distinctly pocketed in *H. suspectum* and *H. matthewi* than in *H. horridum.* The maxilla in *H. horridum* covers part of the dorsal surface of the head whereas in *H. suspectum* and *H. matthewi* the maxilla is not as strongly deflected to the dorsum of the skull. These relative differences indicate that the preorbital region of *H. horridum* tends to be more inflated compared to the more flattened or depressed snout of *H. suspectum* and *H. matthewi.*

The palatal shelf of the maxilla is essentially horizontal in the living species with most of the tooth crown projecting below the ventral border. In *H. matthewi* the palatal shelf has a distinct ventroexternal slope, which produces an arched palatal shelf. As a result, in *H. matthewi* less than half the tooth shaft length projects below the ventral border of the maxilla. Anteriorly the palatal shelf in the living species has a distinct ventral projection that articulates with the septomaxilla near the anterior end. This shelf tends to isolate the first three or four maxillary teeth in a pit, and is more distinct in *H. horridum* than in *H. suspectum.* In *H. matthewi* this ventral projection is essentially absent.

The most obvious difference between *H. matthewi* and the living species is in the shape of the frontal (Fig. 2A). In the living species the outline of the frontal has the shape of a parallelogram

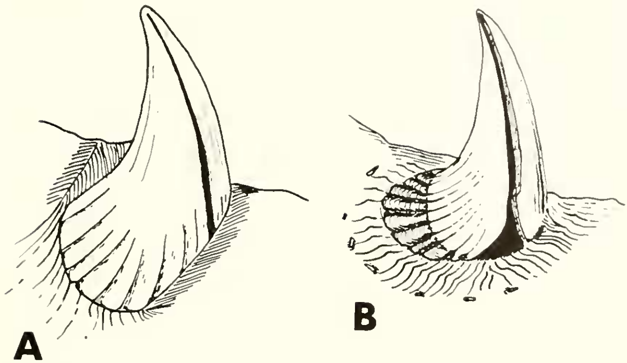

FIG. 3.—*Heloderma* maxillary teeth. A. *Heloderma matthewi,* UNSM 50011, 5th maxillary tooth, lingual view, ventral to top; B. *Heloderma suspectum,* KU 23009, 4th maxillary tooth, lingual view, ventral to top. Approximately × 12.

(see McDowell and Bogert, 1954: Fig. 35) with a relatively flat anterior end, whereas in *H. matthewi* the frontal is triangular in outline with a decidedly pointed anterior end. This triangular-outlined frontal shape is very similar to that found in *Arpadosaurus* (Meszoely, 1970) and some species of *Glyptosaurus* (Gilmore, 1928:185). The continuous anterior sutures suggest that the external naris in *H. matthewi* probably did not extend back to the frontal as it does in the living species. The granular-textured osteoscutes separated by shallow grooves on the frontal and parietal in *H. matthewi* are smaller than the larger, tuberculate, clearly separated osteoscutes of the living species.

H. matthewi is difficult to separate from *H. gallicum.* The osteoscutes on the parietal of *H. gallicum* (Hoffstetter, 1957: Fig. 5) are very similar to those of *H. matthewi,* while the osteoscutes on the maxilla (Hoffstetter, 1957: Fig. 2) are less distinctly separated than those of *H. matthewi.* The degree of development of the venom groove in *H. matthewi* is not significantly different from that found in *H. gallicum* (Hoffstetter, 1957: Fig. 2A′). The length of the parietal of *H. gallicum* is no longer than in the similar-sized Gila monster, *H. suspectum,* and is somewhat shorter than the larger-sized beaded lizard, *H. horridum* (Table 1). *H. gallicum* has 11 or 12 maxillary teeth and *H. matthewi* has 11. Unfortunately the frontal of *H. gallicum* is not known, so comparison with *H. matthewi* is not possible. The only derived feature that is useful to separate *H. gallicum* from *H. matthewi* and the living species, is the narrowness of the parietal in the middle part. The parietal of *H. gallicum* is definitely more constricted in the middle part than in the living species. The parietal of *H. matthewi,* although incomplete, also seems to be less constricted in the middle part than in *H. gallicum.*

TABLE 1.—MEASUREMENTS OF THE MAXIMUM ANTEROPOSTERIOR LENGTH OF THE PARIETAL OF *H. gallicum*, *H. suspectum* AND *H. horridum*.[1]

	Number	*Range*	*Mean ± Standard Error*
H. gallicum	3	19-22.5	20.5
H. suspectum	13	19.4-26.5	21.4±.6
H. horridum	4	25.1-30.5	27.1

[1] Measurements taken from anterior border of parietal to point of juncture of parietal and exoccipital; measurements for *H. gallicum* taken from Hoffstetter (1957: Fig. 5).

Differences in the nature of the intramandibular septum may prove useful to separate *H. gallicum* and *H. matthewi* from the living species when more fossils are available. The ventral border of the intramandibular septum appears to be partially free in *H. gallicum* (see Hoffstetter, 1957: Fig. 3B). This feature in association with a non-vertical posterior border of the dentary and a coronoid overlap of the dentary suggest that *H. gallicum* may not have had a mandibular hinge (an unusual condition for a varanoid lizard). *H. matthewi* also has a tiny, partially free ventral border of the intramandibular septum, possibly indicating that *H. matthewi* also lacked a mandibular hinge. Even though the ventral border of the intramandibular septum is fused to the floor of the Meckelian groove, *H. suspectum* has no mandibular hinge (McDowell and Bogert, 1954:108). There is a rudimentary dentary-surangular hinge found in *H. horridum*. The absence of the mandibular hinge is probably primitive for *Heloderma*, reflecting its basal position among varanoids as interpreted by McDowell and Bogert (1954: Fig. 42).

Relationships Between Helodermatid Lizards

In order to determine the relationships between the four helodermatid species, the primitive and derived conditions for 11 variable characters were coded (Table 2). These characters are:

1. *Number of maxillary teeth.* Three distinct character states are recognized and coded in a linear series: 11–12 (State 0); 8–9 (State 1); 6–7 (State 2). The widespread tendency for the reduction in the number of maxillary teeth in varanoid lizards suggests that State 0 is the primitive condition; State 2 is the most derived.

2. *Number of dentary teeth.* Two character states are recognized: 12–13 (State 0); 8–10 (State 1). State 0 is considered primitive because of the tendency for reduction in the number of teeth among varanoid lizards.

3. *Groove for the conduction of venom.* The presence of a venom groove in lizards is unique to helodermatids. Two states of the groove for the conduction of venom are recognized: groove essentially closed at the base of the tooth (State 0); and groove broadly

open at the base of the tooth (State 1). Since all helodermatid lizards have a venom groove developed on the teeth, the least well-developed condition (State 0) is considered primitive.

4. *Shape of osteoscutes.* The occurrence of non-imbricating osteoscutes over the entire head among varanoid lizards is unique to helodermatid lizards and a few fossil varanoids (i.e., Parasaniwidae), while most anguioid lizards have imbricating to non-imbricating osteoscutes covering the entire head. Two distinct character states exist among helodermatids: low, granular-textured osteoscutes (State 0); and pustulate-textured osteoscutes (State 1). State 0 is most like the condition found in other anguimorphan lizards and is thus taken as the primitive state for helodermatids.

5. *Grooves between maxillary osteoderms.* Three conditions are recognized: no grooves (State 0); shallow grooves (State 1); and deep grooves (State 2). State 0 is considered primitive because it is the least well-developed condition.

6. *Parietal. Heloderma gallicum* has a much constricted parietal at the middle part (State 1), whereas *H. matthewi*, *H. suspectum* and *H. horridum* are much less constricted (State 0). Most anguimorphan lizards have non-constricted parietals, which is thus taken as the primitive state.

7. *Nasal process of the maxilla.* In almost all anguimorphan lizards the nasal process of the maxilla rises at less than 90 degrees (State 0). Only in *Shinisaurus*, *Xenosaurus* and *H. horridum* is the rise nearly perpendicular or slightly curved anteriorly (State 1). The widespread occurrence of State 0 is believed to be primitive.

8. *Mandibular hinge.* Among living varanoid lizards only *H. suspectum* lacks a mandibular hinge (State 0). All anguioid lizards also lack a mandibular hinge. *H. gallicum* and *H. matthewi* may

TABLE 2.—TAXONOMIC DISTRIBUTION OF HELODERMATID CHARACTER STATES.[1]

Character	*gallicum*	*matthewi*	*suspectum*	*horridum*
1	0	0	1	2
2	0	?	1	1
3	0	0	1	1
4	0	0	1	1
5	0	1	2	2
6	1	0	0	0
7	0	0	0	1
8	0	0	0	1
9	1	1	2	2
10	?	?	1	0
11	?	1	0	0
Total Score	2	3	9	11

[1] State 0 is the primitive condition and States 1 and 2 are derived; a query indicates the character is not observable in that taxon.

have lacked a mandibular hinge. The only helodermatid that possesses a mandibular hinge is *H. horridum* (State 1). Since the absence of the mandibular hinge is the most widespread condition found among helodermatids, it is considered primitive.

9. *Posterior border of the intramandibular septum.* This structure is related to the development of the mandibular hinge. A totally free posterior border of the intramandibular septum (State 0) occurs in all anguioid lizards. In *H. gallicum*, *H. matthewi*, and the Parasaniwidae (Estes, 1963:128) the posterior border of the intramandibular septum is partially free (State 1), while all other varanoid lizards and *H. suspectum* and *H. horridum* have the posterior border of the intramandibular septum completely fused to the floor of the Meckelian groove (State 2). State 0 is assumed to be primitive for anguimorphan lizards considering its occurrence in the more primitive anguioids and its inferred functional prerequisite for States 1 and 2; State 2 is the most derived.

10. *Palatine teeth.* Among varanoid lizards only *H. horridum*, *Saniwa* and *Lanthanotus* possess palatine teeth (State 0). The presence of palatine teeth is primitive for reptiles and probably for lizards (Camp, 1923:366). The lack of palatine teeth (State 1) in *H. suspectum* is probably derived.

11. *Frontal shape.* A triangular-outlined frontal (State 1) is not common among anguimorphan lizards. Most anguimorphan lizards have a parallelogram-outlined frontal (State 0), although often the frontal is elongate, giving the impression of triangularity. State 0 is most like the condition found in other anguimorphan lizards and is considered the primitive condition.

The derived state for five of the 11 variable characters (6, 7, 8, 10, 11) is unique to one species (not the same species for each character); they therefore provide no evidence of relationship, although they are useful taxonomic characters.

The taxonomic distribution of the remaining 6 characteristics indicate two distinct groupings: *H. gallicum* and *H. matthewi*, characterized by the presence of mostly primitive characters; and *H. suspectum* and *H. horridum*, characterized by the presence of mostly derived characters. *H. gallicum* is the most primitive helodermatid because of the presence of 10 of 11 characteristics exhibiting primitive states. *H. gallicum* is very closely related to, and difficult to separate from *H. matthewi*. *H. matthewi* possesses only a single derived character (State 1 for character 5) over *H. gallicum*. The morphologic gap, considering only the variable characters, between the *H. gallicum*-*H. matthewi* and the *H. suspectum*-*H. horridum* groupings is considerable, although their overall morphologic similarity, considering non-variable characters, suggests a close phylogenetic relationship. The derived state for characters 1, ?2, 3, 4, 5, and ?9 are shared by *H. suspectum* and *H. horridum*, indicating that these two helodermatids are closely related. The

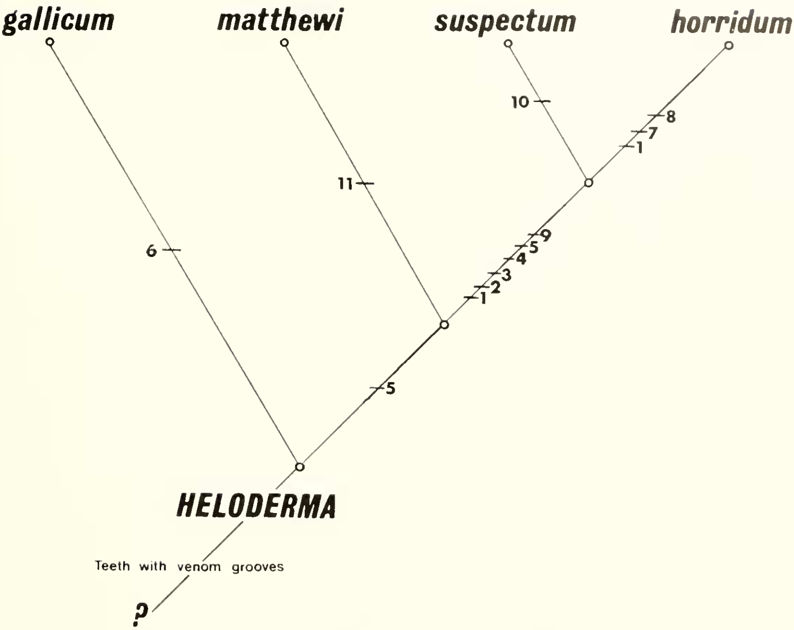

FIG. 4.—Relationships of *Heloderma* species. Numbers refer to character state shifts for numbered characteristics (Table 2). Diagram illustrates only relative position of common ancestor.

development of derived characters for characters 1, 7, 8 in *H. horridum* indicates it is the most specialized of the living species. Figure 4 illustrates the relationships of the four helodermatid lizards.

CONCLUSIONS

New fossil *Heloderma* specimens from Oligocene sediments in Colorado and Nebraska add to our knowledge of and confirm Gilmore's separation of *H. matthewi* from the living species, *H. suspectum* and *H. horridum*. The close morphologic similarity between *H. matthewi* Gilmore, 1928, and *Eurheloderma gallicum* Hoffstetter, 1957, suggests that *Eurheloderma* is a junior synonym of *Heloderma*.

The free posterior border of the intramandibular septum, and the inferred lack of a mandibular hinge in *H. gallicum*, and probably also in *H. matthewi*, and the lack of a mandibular hinge in *H. suspectum* may indicate that *Heloderma* is more closely related to the Anguioidea than to the Varanoidea.

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